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New records of *Leptopilina*, *Ganaspis*, and *Asobara* species associated with *Drosophila suzukii* in North America, including detections of *L. japonica* and *G. brasiliensis*

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Abstract

We report the presence of two Asian species of larval parasitoids of spotted wing Drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), in northwestern North America. *Leptopilina japonica* Novkovic & Kimura and *Ganaspis brasiliensis* (Ihering) (Hymenoptera: Figitidae) were found foraging near and emerging from fruits infested by *D. suzukii* at several locations across coastal British Columbia, Canada in the summer and fall of 2019. While *G. brasiliensis* was found in British Columbia for the first time in 2019, re-inspection of previously collected specimens suggests that *L. japonica* has been present since at least 2016. Additionally, we found a species of *Asobara* associated with *D. suzukii* in British Columbia that is possibly *Asobara rufescens* (Förster) (known only from the Palearctic Region) based on COI DNA barcode data. These findings add to the list of cases documenting adventive es-

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tablishment of candidate classical biological control agents outside of their native ranges. The findings also illustrate the need for revisiting species concepts within *Asobara*, as well as host and geographic distribution data due to cryptic and/or misidentified species.

Keywords
adventive establishment, Braconidae, classical biological control, Drosophilidae, Figitidae, Pteromalidae, spotted wing Drosophila

Introduction

Evidence is accumulating that increasing human activities are responsible for the redistribution of not only invasive pest insects but also many of their natural enemies (Roy et al. 2011; Mason et al. 2017; Weber et al. 2017). In the past few decades, there have been numerous cases where the arrival of invasive insect pests in their invaded range has been followed by the detection of closely associated parasitoids from their native range, which are assumed to be adventive; that is, accidentally introduced (Frewin et al. 2010; Mason et al. 2011, 2017; Talamas et al. 2015; Weber et al. 2017; Ganjisaffar et al. 2018; Stahl et al. 2019). In some cases, at the time of detection, these adventive parasitoids were under consideration for importation and intentional introduction against their pest hosts as classical biological control agents (Mason et al. 2011; Talamas et al. 2015; Abram et al. 2019). These new distribution records are made possible as a result of close collaboration between the biological control and taxonomic communities (Rosen 1986; Rosen and DeBach 1973; Talamas et al. 2015; Buffington et al. 2019).

Spotted wing Drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), is an invasive pest in North America, South America, and Europe that lays its eggs and completes its larval development inside the fruit of a large variety of crop and non-crop host plants (Lee at al. 2011; Asplen et al. 2015; Kenis et al. 2016). A few species of resident pupal parasitoids, including *Pachycrepoideus vindemmiae* Rondani (Hymenoptera: Pteromalidae), were found attacking *D. suzukii* in these invaded areas but parasitism levels were generally low (Lee et al. 2019). Larval parasitism of *D. suzukii* in invaded areas appears to be particularly uncommon, probably due to the inability of most genotypes of native larval parasitoids to overcome the immune defenses of *D. suzukii* (Lee et al. 2019; Kacsoh and Schlenke 2012; Poyet et al. 2013). Thus, soon after the introduction and spread of *D. suzukii* in invaded areas, exploration for potential classical biological control agents in China, South Korea, and Japan began with the goal of identifying parasitoid species that could be evaluated as potential classical biological control agents (Daane et al. 2016; Girod et al. 2018a; Giorgini et al. 2019). These surveys found several parasitoid species attacking *D. suzukii* larvae and pupae, but two larval parasitoids were responsible for the greatest levels of parasitism: *Ganaspis brasiliensis* (Ihering) and *Leptopilina japonica* Novkovic & Kimura (Hymenoptera: Figitidae). These two species both parasitize early-instar larvae of *D. suzukii* inside fresh fruit (Wang et al. 2018), although *L. japonica* will also attack hosts in other substrates (e.g., banana traps) (Daane et al. 2016; Giorgini et al. 2019). *Leptopilina japonica* is known to attack Drosophilidae other than *D. suzukii* in the field in Asia (Novković et al. 2011). *Ganaspis brasiliensis* has only been reared from fresh fruits infested by *D. suzukii* and other closely related, microsympatric frugivorous Drosophilidae and thus appears to have a more restricted host range than *L. japonica* (Daane et al. 2016; Girod et al. 2018a; Giorgini et al. 2019). The host specificity of *G. brasiliensis* may also vary significantly among genetic lineages (Nomano et al. 2017; Girod et al. 2018b). Recently, *G. brasiliensis* was reared from sentinel traps containing larvae and pupae of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) in Mexico (Gonzales-Cabrera et al. 2020), representing the first time this species has been detected in continental North America.

Exploration for biological control agents of *D. suzukii* has also led to the discovery of described and several undescribed species of *Asobara* (Hymenoptera: Braconidae) attacking *D. suzukii* in Asia (Nomano et al. 2015; Guerrieri et al. 2016). *Asobara japonica* Belokobylskij was initially considered as a potential classical biological control agent of *D. suzukii* but was subsequently excluded from consideration due to its relatively broad host range (Daane et al. 2016; Girod et al. 2018b). Both Asian and European lines of another species in the same genus, *Asobara tabida* Nees, failed to develop on *D. suzukii* in laboratory experiments (Chabert et al. 2012; Nomano et al. 2015). North American *Asobara* species are not presently known to parasitize *D. suzukii*, although one species (putatively *A. tabida*) has been observed in a possible association with *D. suzukii* (Thistlewood et al. 2013).

In this article, we report the unexpected presence of both *L. japonica* and *G. brasiliensis* in northwest North America, representing the first time they have been detected in this area. These are the first records of *G. brasiliensis* in North America outside of Mexico, and the first records of *L. japonica* outside of its presumed native range of Asia. We also report one species of *Asobara* (Hymenoptera: Braconidae), as well as *Pachycrepoideus vindemmiae* (Hymenoptera: Pteromalidae), in probable association with *D. suzukii*.

Materials and methods

Preliminary parasitoid collections

On July 15, 2019, we first observed numerous parasitoids walking on and flying in the vicinity of raspberry (*Rubus idaeus* 'Rudi') fruits in an experimental plot heavily infested by *D. suzukii* in Agassiz, British Columbia, Canada (GPS: 49°14'34.8"N, 121°45'18.0"W). Remarkably, we collected > 100 parasitoid specimens by mouth aspirator in less than 45 min of effort by two individuals (PKA, personal observations). We also collected 20 raspberry fruits presumed to be infested by *D. suzukii*, which were divided between two ventilated plastic containers (0.25 L) with filter paper to observe whether any parasitoids successfully emerged. A subset of field-collected parasitoid individuals were exposed to 2nd and 3rd-instar *D. suzukii* larvae (approx. 50 per vial) in two *Drosophila* rearing vials containing artificial diet (Formula 4–24 medium, Carolina Biological Supply Co. Burlington, NC) to informally test whether or not they were capable of successfully parasitizing *D. suzukii* larvae. Parasitoids emerged both from field-collected *D. suzukii*-infested raspberries and lab-reared *D. suzukii* larvae in artificial diet exposed to field-collected parasitoid adults (PKA, personal observations). This was surprising, given the known low developmental success of North American larval parasitoids attacking *D. suzukii* (Lee et al. 2019). This observation motivated an attempt to obtain a preliminary species-level identification. A 683 bp region of the cytochrome oxidase I (COI) gene of one aspirator-collected parasitoid specimen was barcoded and compared against existing records in GenBank using a nucleotide BLAST (NCBI, 2019). This sequence showed 98.67 % identity with GenBank Accession AB546875.1, which is a sequence of *L. japonica* from Japan (Novkovic et al. 2016). Specimens from the same date and location that were collected by mouth aspirator (n = 24), emerged from raspberry fruit (n = 3), and that emerged from lab-reared *D. suzukii* larvae (n = 6), were all identified as *L. japonica* (by MLB) based on morphology (see *Identification of parasitoid specimens* below for details on morphological determinations). This initial find prompted a re-examination of parasitoid specimens (n = 14) emerging from 60 *D. suzukii*-infested strawberry (*Fragaria × ananassa*) fruits (total n = 375 emerging *D. suzukii*) collected near Langley, British Columbia in two commercial fields (GPS: 49°07'34.7"N, 122°32'45.2"W and 49°08'07.8"N, 122°33'42.1"W) between September 20 and 27, 2016. Based on morphology, the parasitoid specimens were also confirmed to be *L. japonica*, suggesting that this species has been present in British Columbia since at least 2016.

Parasitoid collections throughout southwestern British Columbia

Motivated by the unexpected detection of *L. japonica* in British Columbia, we next conducted additional collections in 2019 to determine how widespread in coastal British Columbia *L. japonica* might be, and whether any other native or exotic species of parasitoids might also be present. From August to October 2019, parasitoid specimens were obtained from 54 opportunistic collection samples from 23 different sites in coastal British Columbia (the lower mainland and Vancouver Island) (Fig. 1). Parasitoid specimens (n = 525) were collected from plants and areas known to be infested by *D. suzukii* with one of three sampling methods: (1) mouth aspiration of parasitoids seen flying or resting on the foliage or fruits of Himalayan blackberry, *Rubus armeniacus* (n = 34 samples) or cultivated blackberry, *Rubus fruticosis* 'Triple Crown' (n = 2 samples); (2) collection of *R. armeniacus* fruits (approx. 20–60 berries per sample) into ventilated plastic rearing containers (volume: 0.5 or 1.0 L) lined with filter paper to rear out parasitoids and host Drosophilidae in the laboratory (16:8 hour light:dark, 24 ± 1 °C) (n = 14); (3) separation of parasitoid by-catch from plastic traps baited with apple cider vinegar placed in hedgerows on a university experimental farm to collect *D. suzukii* (n = 2); and (4) collection of *R. armeniacus* berries followed by exposure outside in a plastic trap for 6 days, and then rearing out insects in glass jars in the laboratory (n = 2). Collections from *R. armeniacus* were in suburban or natural areas along roadways or in parks. For a subset of 14 *R. armeniacus* fruit collections from which at least one parasitoid emerged, emerging Drosophilidae (n = 1,637) were also counted and identified. All identifiable emerged Drosophilidae were either *D. suzukii* (85.8 %) or *D. melanogaster* (0.6 %). Remaining flies (13.6 %) could not be identified conclusively due to deterioration or mold in containers. Full information on collection sites, dates, and methods, and insect emergence if applicable, can be found in the Suppl. material 1. Due to the opportunistic nature of our sampling in space and time, and unknown levels of parasitoid and host mortality in rearing, we did not calculate or present percent parasitism levels. All collected parasitoids were preserved in 95 % EtOH for subsequent morphological and molecular identification.

Identification of parasitoid specimens

Specimens from both initial and more extensive collections in British Columbia were sent to MLB after initial COI barcoding (by SJP and CC) yielded results consistent with barcode sequences on GenBank under the name *L. japonica* (see above). Upon further examination, it was determined that not only was *L. japonica* present in the samples but so too were *G. brasiliensis*, an undetermined species of *Asobara*, and *P. vindemmiae* (Figs 2–7). Specimens of *L. japonica* and *G. brasiliensis* were vacuum dried and card mounted; the *Asobara* and *Pachycrepoideus* specimens were prepared using HMDS (Heraty and Hawks 1998) and point mounted. Specimens are deposited in the insect collection of the National Museum of Natural History (**USNM**; Smithsonian Institution, Washington DC) and the Canadian National Collection of Insects, Arachnids, and Nematodes (Ottawa, Ontario, Canada).

The morphology-based research in Novković et al. (2011), Buffington and Forshage (2016) and Lue et al. (2016), as well as specimens in the USNM, were used to confirm the identities of the Figitidae. While this research was being conducted, it became clear that specimens of *Leptopilina* submitted to MLB for identification in 2016 were misidentified as *Leptopilina heterotoma* (Thompson). At that time, the USNM lacked specimens of *L. japonica*, making a direct comparison impossible. Recently, the USNM has received voucher specimens from the original paper describing *L. japonica*, as well as additional material from China and Korea. This made direct comparisons possible, and the identity of the 2016 specimens was corrected.

In terms of Figitidae attacking *D. suzukii*, *L. japonica* and *G. brasiliensis* can be difficult to distinguish (Figs 2, 3). Careful examination of the posterior aspect of the metapleuron reveals a complete patch of setae in *G. brasiliensis* (Fig. 4a), while the same location in *L. japonica* is glabrous (Fig. 5a). Additionally, the metasoma setal hair ring is complete in *G. brasiliensis* (Fig. 4b) and dorsally incomplete in *L. japonica* (Fig. 5b). Lastly, the metapleuron, in lateral view, is simple in *G. brasiliensis* (Fig. 4c); in *L. japonica*, a longitudinal carina transverses the middle of the metapleuron (Fig. 5c).

Specimens of *Asobara*, *Pachycrepoideus*, and Figitidae are relatively easy to differentiate from one another given their overall dissimilar shape and color (Figs 6, 7).

The single Pteromalidae specimen was identified and confirmed using Bouček and Heydon (1997) and by comparison with authoritatively identified specimens in the USNM. The specimens of *Asobara* were sight identified to genus; Wharton (1980), Vet et al. (1984), and Nomano et al. (2015) were consulted in an effort to identify the specimens to species.

A subset of the Figitidae and Braconidae specimens were sequenced for the COI 'barcode' region; as only one *Pachycrepoideus* was collected, no barcode was generated for this species. DNA was extracted using the QIAamp DNA Micro Kit (Qiagen). PCR amplifications of COI were carried out using LCO1490 (Folmer et al. 1994) and C1-N-2191 (Simon et al. 1994) with a Bio-Rad T100 thermal cycler under the following cycling conditions: initial denaturation for 7 min at 95 °C, 35 cycles of 30 s at 95 °C, 30 s at 50 °C, 45 s at 72 °C, and a final extension for 1.5 min at 72 °C. PCR products were cleaned with ExoSAP-IT (Affymetrix), sequenced with BigDye v.3.1 (Life Technologies) and run on an ABI 3730xl automated DNA sequencer (Applied Biosystems). Contigs were assembled and edited in Geneious Prime 2020.04 (Biomatters). Sequences used in the study have been deposited in GenBank (Accession nos. MT559416–MT559426).

Results and discussion

Figitidae

Leptopilina japonica was the most common parasitoid species found in our collections, representing 95.8 % (503/525) of all parasitoids we collected and identified in British Columbia in 2019. This species was present across the sampled area (Fig. 1) and was collected with all three sampling methods (traps, aspirator collections, rearing from infested fruit). *Ganaspis brasiliensis* was the next most common species (2.7 % of all specimens) and was present at three sites, which were all in the eastern part of the sampled geographic range (Fig. 1). This species was collected both with aspirators while foraging on berries and emerging from *D. suzukii*-infested berries. Somewhat surprisingly, no native *Leptopilina* spp. were found in our samples in 2019.

Results from DNA barcoding of a small subset of Figitidae specimens was consistent with all morphologically-based identifications. COI sequences from *L. japonica* showed high similarity to specimens previously collected in China and Japan (> 98 % identity). All four of the *G. brasiliensis* specimens from British Columbia that we barcoded clustered within the "G1" clade (100 % identity), which has previously been found in South Korea, China, and Japan (Nomano et al. 2017; Giorgini et al. 2019) and appears to be the most host-specific lineage of *G. brasiliensis* (Nomano et al. 2017; Girod et al. 2018b). Further studies are needed to determine the levels of genetic diversity of *L. japonica* and *G. brasiliensis* in North America and potential source populations of these parasitoids in Asia.

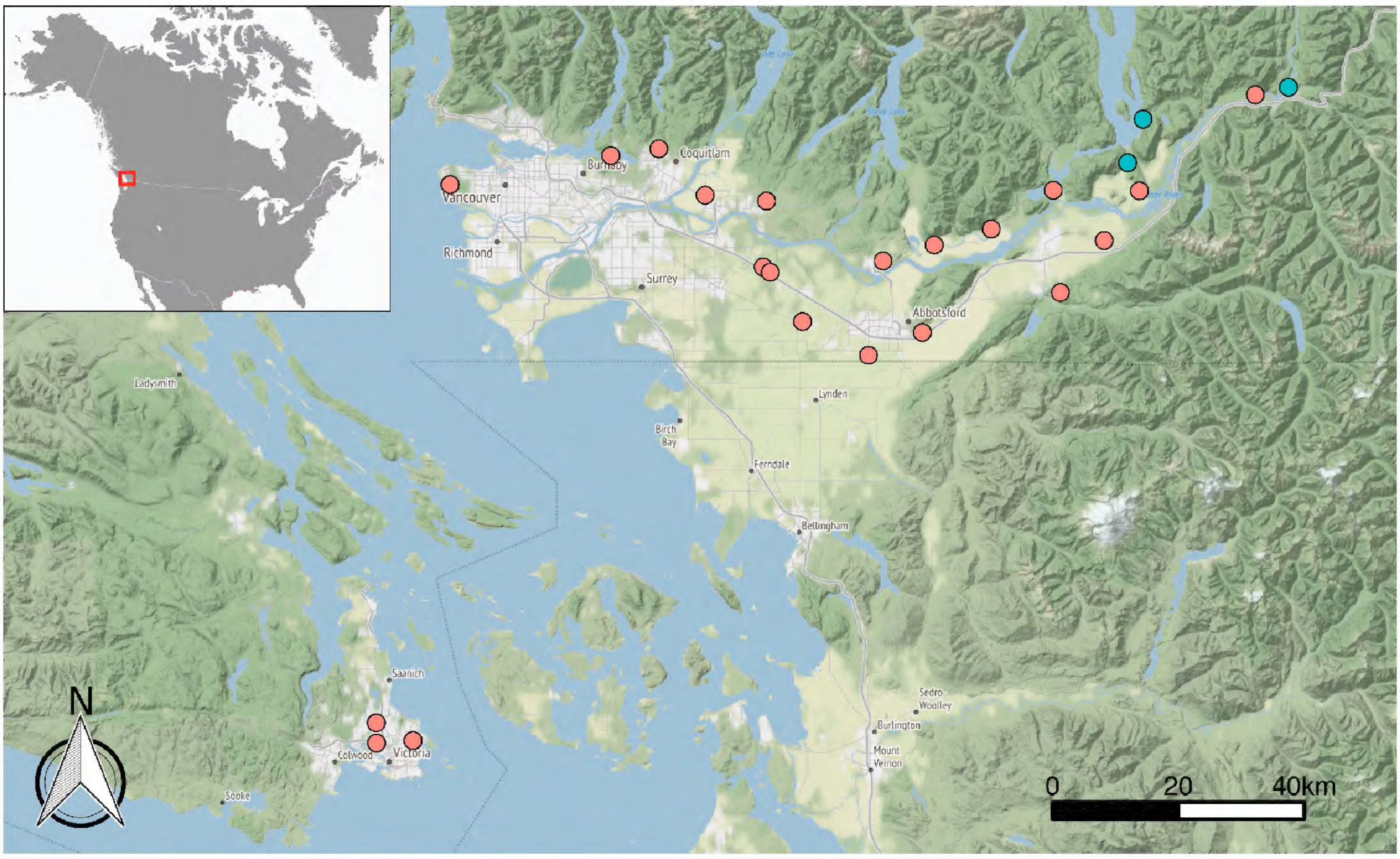
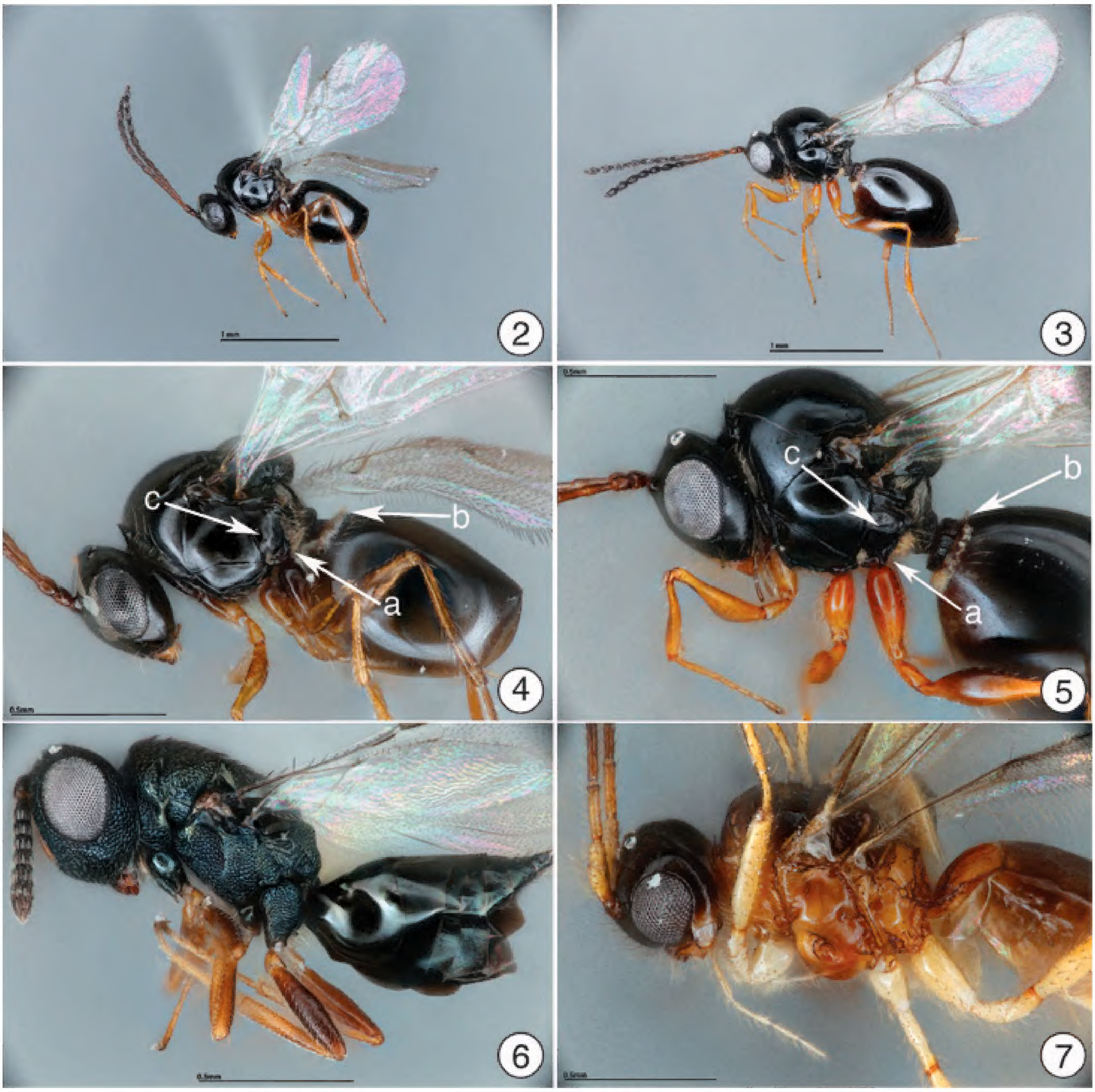


Figure 1. Map of sites where *Leptopilina japonica* (red circles), or both *L. japonica* and *Ganaspis brasiliensis* (green circles) were found in British Columbia, Canada in 2016 and 2019. The red box in the inset shows where the mapped area is situated in North America. Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

We emphasize that because our sampling took place within a restricted time window and set of habitats, our data are likely not representative of the two adventive figitid parasitoid species' relative abundances or impact. They simply demonstrate that these two species are present in the south coastal region of British Columbia. More widespread, season-long surveys in several habitats are needed to determine the relative abundance and distribution of each species. Similarly, repeated fruit collections containing known life stage distributions of hosts, coupled with population modelling approaches such as stage-structured matrix models (e.g., Wiman et al. 2014, 2016), will be necessary to estimate the population-level impact of these adventive exotic parasitoids attacking *D. suzukii* – and possibly other, non-target Drosophilidae – in North America.

Braconidae

One species of *Asobara* (1.5 % of all parasitoids in collections) was collected with aspirators from berries (n = 3) and reared from *D. suzukii*-infested blackberries (n = 5) from two sites. Although nearly all of the Drosophilidae emerging from these collections were *D. suzukii*, we cannot exclude the possibility that the five *Asobara* that emerged from berries could have been associated with *D. melanogaster*, which was present at very low levels in our samples (see above). Exposure of three female *Asobara* to lab-reared *D. suzukii* larvae in artificial diet (see methods in "Preliminary parasitoid



Figures 2–7. *Ganaspis brasiliensis* (**2, 4**); *Leptopilina japonica* (**3, 5**); *Pachycrepoideus vindemmiae* (**6**); *Asobara* sp. (**7**).

collections" above) only yielded a single male offspring (PKA, personal observations). While the field collections and single lab observation provides a proof-of-concept that this *Asobara* species can attack and develop in *D. suzukii*, at this time the association of this *Asobara* species with *D. suzukii* should be considered tentative. As far as is known, species of *Asobara* are solitary koinobiont endoparasitoids of cyclorrhaphous flies, mostly Drosophilidae (Wharton 1997, Yu et al. 2016).

Two species of *Asobara*, *A. tabida* (Nees) and *A. fungicola* (Ashmead), are known from the Nearctic Region, and both species have been reported from British Columbia (Yu et al. 2016). One of us (RRK) initially identified the *Asobara* we found associated with *D. suzukii* in British Columbia as *A. tabida* using Wharton (1980), but *A. tabida* and *A. fungicola* are the only species included in the key. Several species of *Asobara*, including *A. tabida* and *A. fungicola*, occur in multiple zoogeographic regions (Yu et al.

2016). Therefore, it is possible that other *Asobara* species morphologically similar to *A. tabida* and *A. fungicola* occur in the Nearctic Region but are commonly misidentified as the aforementioned species. For example, *Asobara rufescens* (Förster) and *A. tabida* are extremely similar morphologically; Vet et al. (1984) considered them sibling species and identified subtle differences in color, shape of antennal flagellomeres 1 and 2, tarsal claw length, and the basitarsus. *Asobara rufescens* (Förster, 1863) is currently known only from the Palearctic Region but has been considered a junior synonym of *A. tabida* (Nees, 1834), which occurs in the Nearctic, Palearctic, Oriental, and Oceanic regions. Thus, if *A. rufescens* occurs in the Nearctic Region it could be easily misidentified as *A. tabida*, especially when using identification tools that were based on region or published during the period of time when *A. rufescens* was a junior synonym of *A. tabida*. Recent efforts to accurately identify species of *Asobara* have relied on COI DNA barcoding along with authoritative identifications based on morphological features (Nomano et al. 2015, Guerrieri et al. 2016).

We obtained a 658-bp fragment of the COI DNA barcoding region from one of the specimens RRK tentatively identified as *A. tabida*. A GenBank nucleotide BLAST search (NCBI 2019) using the 658-bp fragment, as well as a search of all COI barcode records using the Identification System in the Barcode of Life Database (BOLD; Ratnasingham and Hebert 2007), yielded 53 COI sequences we consider conspecific with our *Asobara* specimen. Of the 41 sequences from GenBank, 39 had 98.79–100 % identity (79–100 % query coverage) with the *Asobara* COI sequence obtained in this research; percent identities for the two most dissimilar sequences that we still consider conspecific were 97.24 % and 97.26 % (100 % and 93 % query coverage, respectively). The 41 sequences from GenBank were mostly from specimens identified as *A. rufescens* (n = 36) but also included some identified only as Braconidae or Hymenoptera (n = 5). The sequences in BOLD consisted of the 41 recovered via GenBank and an additional 12 sequences we consider conspecific with our *Asobara* species. Of the 53 sequences recovered, 51 have sequence similarity ranging from 99.18–100 %, and two have sequence similarity ranging from 97.19–97.22 %; all are in BOLD under the name *A. rufescens*. One sequence in both GenBank and BOLD under the name *A. rufescens* (GenBank: KT604569.1) appeared to have quality control issues and was not considered in this research. The most similar sequence in GenBank and BOLD that we do not consider conspecific was from a specimen identified as *A. tabida*, with 93.46 % identity (99 % query coverage) in GenBank and 93.36 % similarity in BOLD relative to our *Asobara* sequence.

Sequences in BOLD/GenBank identified as *A. rufescens* were likely determined as such based solely on their high similarity to sequences already in those databases from specimens identified as *A. rufescens* using morphological features. Notably, COI sequences from putative *A. rufescens* specimens from Japan (Nomano et al. 2015; GenBank: AB920758.1, AB920759.1, AB920763.1, AB920762.1), identified by M. Kimura using the morphological features from Vet et al. (1984), are likely the basis for all subsequent COI sequence identifications in BOLD/GenBank. If the specimens from Japan are accurately identified as *A. rufescens*, a specimen of *A. rufescens* collected in Puslinch, Ontario, Canada on August 14, 2008 (Hebert et al. 2016; GenBank: KR884537.1) would be the first record of *A. rufescens* in the Western Hemisphere. Further, collection data for all sequences in BOLD/GenBank putatively conspecific with M. Kimura's *A. rufescens* reflect that this species was collected in Canada every year from 2008–2019 (except 2011) with occurrences ranging from Forillon National Park, Quebec (Hebert et al. 2016; GenBank: KR420364.1) to Elk Island National Park, Alberta (Hebert et al. 2016; GenBank: KR793444.1). Thus, *A. rufescens* has possibly occurred in North America since at least 2008, the year *D. suzukii* was first detected on the continent (Asplen et al. 2015), and ranges from east to west across nearly all of Canada. Thistlewood et al. (2013) reported specimens of *Asobara* reared from fermenting banana that was artificially infested with *D. suzukii* and then placed in the field in British Columbia, which they considered likely to be *A. tabida*. The *Asobara* specimens reported in Thistlewood et al. (2013) might be conspecific with our *Asobara* species from British Columbia. If so, it is possible that our *Asobara* species (possibly *A. rufescens*) has been associated with *D. suzukii* since at least 2011; however, this is uncertain regardless of *Asobara* species identity because the banana baits were infested with Drosophilidae other than *D. suzukii* after being placed in the field.

Kimura's identification of *A. rufescens* from Japan, based on the morphological features identified in Vet et al. (1984) for differentiating *A. rufescens* and *A. tabida* (Nomano et al. 2015, M. Kimura personal communication), should be considered tentative. Features used by Vet et al. (1984) lack enough detail to reliably differentiate species of *Asobara* that are, perhaps, morphologically cryptic (R. Kula personal observation). The features used were differences, "in the shape of the 3rd and 4th antennal segment… and in the relative length of the claws," as well as unspecified differences "in the colour" and "in the basitarsus of the hind legs" (Vet et al. 1984). These features might reflect differences between *A. rufescens* and *A. tabida*, but accurate interpretation is difficult because the color differences were not illustrated or specified, the basitarsus difference was not elaborated or quantified, and the shape and length differences in the flagellomeres and tarsal claws, respectively, were not quantified. Line drawings were used to illustrate the relevant portions of the antenna and tarsus for specimens Vet et al. (1984) considered *A. rufescens* and *A. tabida*, as well as an *A. rufescens* × *A. tabida* hybrid; thus, identification requires interpreting subtle differences in the line drawings by eye and without consideration for potential intraspecific variation. Thus, the features identified in Vet et al. (1984) require additional assessment to determine their utility.

Beyond morphological features, Vet et al. (1984) discerned via olfactometer tests that what they initially considered *A. tabida* actually consisted of two species attracted to different host habitats. One of the species was attracted to the odor of fermenting fruit, while the other species was attracted to the odor of decaying leaves, thus resulting in a premating reproductive barrier. The authors discerned, through comparison of their *Asobara* specimens with the holotype of *A. rufescens* for aforementioned morphological features, that the specimens attracted to decaying leaves were *A. rufescens*. Thus, the authors regarded *A. tabida* as a parasitoid of frugivorous Drosophilidae and *A. rufescens* as a parasitoid of saprophagous Drosophilidae. Mitsui et al. (2007) reported

A. tabida and *A. rufescens* from Drosophilidae, including the former from *D. suzukii*, infesting clumps of banana placed at field sites; they also reported *A. rufescens* from *Scaptomyza pallida* (Zetterstedt) in decaying leaves. However, Chabert et al. (2012) found that *A. tabida* rarely oviposits into *D. suzukii*. Other research has shown, based on analysis of COI DNA barcoding data, that other *Asobara* specimens perceived as conspecific are apparently complexes of morphologically similar species (Nomano et al. 2015, Guerrieri et al. 2016) with different patterns of host use. Thus, additional research is needed to discern the limits of species in *Asobara*, as well as patterns of host use and factors that affect those patterns.

The COI sequence from our *Asobara* species from British Columbia was also very similar to COI sequences from putative *A. rufescens* collected in Germany (BOLD: 99.28–99.53 % similarity; Matthias et al. 2016) and Japan (GenBank: 99.20–99.24 % identity, 94–100 % query coverage; BOLD: 99.18–99.23 % similarity; Nomano et al. 2015). *Asobara rufescens* has been collected in the Palearctic Region from Japan to the Netherlands (Yu et al. 2016); thus, if the identifications in GenBank and BOLD are accurate, *A. rufescens* is distributed broadly across the entire Holarctic Region. Conversely, while *A. tabida* has been reported across the entire Palearctic Region, from Japan and Russia (i.e., Sakhalin Oblast) west to Ireland, it has been reported infrequently in North America (Wharton 1980, Kraaijeveld and van der Wel 1994, Hoang 2002). Interestingly, there are no COI DNA barcode sequences in either GenBank or BOLD from specimens of *A. tabida* in North America. This raises the possibility that specimens in North America identified previously as *A. tabida* are actually *A. rufescens*. The results reported herein demonstrate the need for discerning species complexes within *Asobara* overall and its implications for interpreting patterns of host use. It would also be useful to sequence nuclear genes in *Asobara*, as some of the confusion in resolving *A. tabida* and *A. rufescens* may be due to hybridization and mitochondrial introgression.

Pteromalidae

Only a single specimen of *P. vindemmiae* was found in our collections. *Pachycrepoideus vindemmiae* is an idiobiont ectoparasitoid recorded as a primary parasitoid of Diptera, Lepidoptera, Hemiptera, and Hymenoptera. Diptera account for most records with 13 families, 33 genera, and 55 species recorded (Noyes 2019). As a facultative hyperparasitoid, hosts include Diptera (Sarcophagidae, Tachinidae) and Hymenoptera (Braconidae, Diapriidae, Encyrtidae, Figitidae, Eulophidae, Pteromalidae). Various factors influence the degree of primary vs. secondary parasitism in *Drosophila* systems (Bezerra Da Silva et al. 2019, Chen et al. 2015, Goubault et al. 2003, Rossi Stacconi et al. 2015, Wang et al. 2016). Related to the work herein, *P. vindemmiae* is known as a parasitoid of *D. melanogaster*, *A. tabida* and *L. heterotoma* (Noyes 2019, Philips 1993, Van Alphen and Thunnissen 1982), and also parasitizes conspecifics (Chen et al. 2015). Future studies could investigate whether *P. vindemmiae* could act as a facultative hyperparasitoid of *L. japonica* and *G. brasiliensis* in North America.

Conclusions

Our findings here add to the growing list of recent high-profile invasive insect pests whose closely associated natural enemies have established adventive populations on new continents (Frewin et al. 2010; Talamas et al. 2015; Mason et al. 2017; Weber et al. 2017; Ganjisaffar et al. 2018; Stahl et al. 2019). Given that we found *L. japonica* to be remarkably common and widespread in our study area, it is quite possible that this species has also established in other areas outside of Asia but has not been detected yet. *Ganaspis brasiliensis* was much less common and widespread in our collections, and until more extensive sampling throughout the entire season is done, we cannot conclude whether or not it is well established in British Columbia. The *Asobara* species (potentially *A. rufescens*) we collected in probable association with *D. suzukii* also merits further investigation, both in terms of its systematics in relation to other *Asobara* worldwide and the extent of its potential impact on *D. suzukii*. We encourage researchers across North America, South America, and Europe to re-evaluate whether these parasitoids may be attacking *D. suzukii* in other invaded areas.

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Supplementary material 1

Collection information for specimens reported in: New records of *Leptopilina*, *Ganaspis*, and *Asobara* species associated with *Drosophila suzukii* in North America, including detections of *L. japonica* and *G. brasiliensis*

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Data type: raw data

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